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# Economic costs of biological invasions in the United Kingdom

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## Abstract

Although the high costs of invasion are frequently cited and are a key motivation for environmental management and policy, synthesised data on invasion costs are scarce. Here, we quantify and examine the monetary costs of biological invasions in the United Kingdom (UK) using a global synthesis of reported invasion costs. Invasive alien species have cost the UK economy between US$6.9 billion and $17.6 billion (£5.4 – £13.7 billion) in reported losses and expenses since 1976. Most costs were reported for the entire UK or Great Britain (97%); country-scale cost reporting for the UK's four constituent countries was scarce. Reports of animal invasions were the costliest ($4.7 billion), then plant ($1.3 billion) and fungal ($206.7 million) invasions. Reported damage costs (i.e. excluding management costs) were higher in terrestrial ($4.8 billion) than aquatic or semi-aquatic environments ($29.8 million), and primarily impacted agriculture ($4.2 billion). Invaders with earlier introduction years accrued significantly higher total invasion costs. Invasion costs have been increasing rapidly since 1976, and have cost the UK economy $157.1 million (£122.1 million) per annum, on average. Published information on specific economic costs included only 42 of 520 invaders reported in the UK and was generally available only for the most intensively studied taxa, with just four species contributing 90% of species-specific costs. Given that many of the invasive species lacking cost data are actively managed and have well-recognised impacts, this suggests that cost information is incomplete and that totals presented here are vast underestimates owing to knowledge gaps. Financial expenditure on managing invasions is a fraction (37%) of the costs incurred through damage from invaders; greater investments in UK invasive species research and management are, therefore, urgently required.

**Abstract in Welsh**

Er bod costau uchel rhywogaethau ymledol yn cael eu nodi'n aml fel rhesymeg allweddol ar gyfer gweithredu polisïau a rheolaeth amgylcheddol, mae data syntheseiddiedig ar gostau ymlediad yn brin. Yma, rydym yn meintioli ac yn archwilio costau ariannol ymlediadau biolegol yn y Deyrnas Unedig (DU) gan ddefnyddio synthesis byd-eang o gostau ymlediadau cyhoeddedig. Mae rhywogaethau ymledol estron wedi costio rhwng UD$ 6.9 biliwn a $17.6 biliwn (£5.4 – £13.7 biliwn) i economi'r DU mewn colledion a threuliau ag adroddwyd ers 1976. Adroddwyd y mwyafrif o gostau ar gyfer y DU neu Brydain Fawr yn ei chyfanrwydd (97%) ac felly roedd adroddiadau costau i'r gwledydd unigol yn brin. Adroddiadau ar ymlediad anifeiliaid oedd yr ymlediadau mwyaf costus ($4.7 biliwn), yna planhigion ($1.3 biliwn), yna ffwng ($206.7 miliwn). Roedd costau difrod yr adroddwyd arnynt (h.y. heb gynnwys costau rheoli) yn uwch mewn amgylcheddau daearol ($4.8 biliwn) nag amgylcheddau dyfrol neu led-ddyfrol ($29.8 miliwn), gan effeithio'n bennaf ar amaethyddiaeth ($4.2 biliwn). Roedd ymledwyr â gyflwynwyd yn gynharach wedi cronni cyfanswm costau ymlediadau roedd yn uwch o lawer 'na rhai a gyflwynwyd yn fwy diweddar. Mae costau ymlediadau wedi bod yn cynyddu'n gyflym ers 1976, gan gostio ar gyfartaledd $157.1 miliwn (£122.1 miliwn) y flwyddyn i economi'r DU. Dim ond ar gyfer 42 o'r 520 o rywogaethau ymledol a gyhoeddwyd costau economaidd penodol yn y DU, a hynny gan amlaf ar gyfer y tacsa a astudiwyd yn fwyaf dwys yn unig, gyda pedair rhywogaeth yn gyfrifol am 90% o'r costau penodol. O ystyried bod llawer o rywogaethau ymledol sydd heb ddata costau yn cael eu rheoli'n weithredol, awgrymir fod gwybodaeth am gostau yn anghyflawn a bod y cyfansymiau a gyflwynir yma ond yn amcangyfrif isel oblegid diffyg gwybodaeth. Mae gwariant ariannol ar reoli ymlediadau yn cynrychioli ffracsiwn (37%) o'r costau a achosir trwy ddifrod gan ymledwyr; felly mae angen buddsoddiadau ychwanegol ar reoli rhywogaethau ymledol y DU ar frys.

**Abstract in Irish**

D'ainneoin gur minic a luaitear na costais arda a bhaineann le hionradh agus gur cúis an-tábhachtach iad le bainistiú agus polasaí comhshaoil, is annamh a fhaightear sonraí sintéisithe faoi chostais ionraidh. Sa pháipéar seo, measaimid ar bhonn cainníochtúil agus scrúdaímid costais airgeadaíochta ionraí bitheolaíochta sa Ríocht Aontaithe (RA) agus leas á bhaint againn as sintéis dhomhanda ar chostais ionraidh a thuairiscítear. Tá geilleagar na RA thíos idir SA$6.9 billiún agus $17.6 billiún (£5.4 – £13.7 billiún) le speicis choimhthíocha ionracha ó bhí 1976 ann maidir le caillteanais agus costais a tuairiscíodh. Is i gcás na RA nó i gcás na Breataine Móire a tuairiscíodh formhór na gcostas agus, mar sin de, is annamh a tuairiscíodh costais ar scála tíre. Ba iad tuairiscí ar ionraí ainmhithe ba mhó a raibh costais ag baint leo ($4.7 billiún), ansin ionraí plandaí ($1.3 billiún) agus ionraí fungasacha ($206.7 milliún). B'airde na costais damáiste a tuairiscíodh (.i. gan costais bhainistithe san áireamh) i dtimpeallachtaí talún ($4.8 billiún), agus tionchar acu seo, go príomha, ar an talmhaíocht ($4.2 billiún), ná i dtimpeallachtaí uisceacha nó leathuisceacha ($29.8 milliún). B'airde i bhfad na costais ionraidh a d'fhabhraigh ionróirí a tugadh isteach ar bhonn níos óige. Tá méadú tapa ag teacht ar chostais ionraidh ó bhí 1976 ann, agus $157.1 milliún (£122.1 milliún) de chostas ar gheilleagar na RA in aghaidh na bliana, ar an mheán mar gheall orthu. Níor chuimsigh eolas a foilsíodh faoi chostais gheilleagracha shonracha ach 42 de chuid na 520 ionróir a tuairiscíodh sa RA agus ní raibh sé ar fáil, go ginearálta, ach i gcás na dtacsón is mó a ndearnadh mionstaidéar orthu, agus gan ach ceithre speiceas bainteach le 90% de na costais sainspeicis. Nuair a chuirtear san áireamh go mbainistítear go gníomhach mórán de na speicis ionracha a bhfuil sonraí costas ina leith ar iarraidh agus go bhfuil tionchair an-aitheanta ag baint leo, tugann sé seo le fios go bhfuil an t-eolas a bhaineann le costais neamhiomlán agus gur meastacháin faoina luach ollmhóra iad, de bharr bearnaí eolais, na hiomláin a chuirtear i láthair anseo. Is cuid bheag (37%) de na costais a thabhaítear de bharr damáiste a dhéanann ionróirí is ea caiteachas airgeadais ar bhainistiú ionraí; tá géarghá, dá réir sin, le hinfheistíochtaí níos mó i mbainistiú speicis ionracha na RA.

### Abstract in French

Bien que les coûts élevés des invasions biologiques soient fréquemment évoqués et qu'ils constituent une motivation clé pour les politiques et la gestion environnementale, les données synthétiques sur ces coûts sont rares. Dans cette étude, nous quantifions et examinons le coût monétaire des invasions biologiques au Royaume-Uni (UK) à l'aide d'une synthèse globale des coûts effectivement reportés. Selon les informations disponibles sur les pertes et les dépenses depuis 1976, les espèces exotiques envahissantes ont coûté à l'économie de l'UK entre 6,9 et 17,6 milliards USD (entre 5,4 et 13,7 milliards £). La plupart des coûts proviennent de l'ensemble de la Grande Bretagne (97%) et, ainsi, les données à l'échelle de chaque pays sont rares. Les invasions animales sont les plus coûteuses (4,7 milliards USD), puis viennent les invasions végétales (1,3 milliard USD) et fongiques (206,7 millions USD). Les coûts des dégâts (i.e. en excluant les coûts de gestion) sont plus élevés dans les environnements terrestres (4,8 milliards USD) que dans les milieux aquatiques ou semi-aquatiques (29,8 millions USD), et concernent majoritairement l'agriculture (4,2 milliards USD). Les organismes envahissants avec des années d'introduction plus précoces sont ceux qui sont associés aux coûts les plus élevés. Le coût des invasions ont augmenté rapidement depuis 1976, avec un coût annuel moyen à l'économie anglaise de 157,1 millions USD (122,1 millions £). Les informations publiées sur des coûts espèce-spécifiques concernent seulement 42 des 520 organismes envahissants connus au Royaume-Uni, et sont généralement disponibles seulement pour les taxons les plus étudiés, avec seulement quatre espèces qui contribuent pour 90% des coûts espèces-spécifiques documentés. Compte tenu du nombre important d'espèces exotiques pour lesquelles il n'existe aucune donnée mais qui sont pourtant activement gérées pour leurs impacts parfaitement reconnus, cela suggère que les informations sur le coût des invasions biologiques sont incomplètes et que les totaux présentés ici sont largement sous-estimés à cause des lacunes de connaissance. Les dépenses liées à la gestion des invasions ne représentent qu'une fraction (37%) des coûts provoqués par les dégâts des espèces exotiques envahissantes. Des investissements plus importants en matière de gestion des espèces envahissantes en UK sont donc nécessaires et urgents pour limiter au maximum les impacts de ces invasions biologiques.

### Abstract in Spanish

Aunque los altos costos de las invasiones se mencionan con frecuencia y son una motivación clave para la gestión y las políticas ambientales, aún las síntesis de datos de los costos de las invasiones son escasas. Aquí, cuantificamos y examinamos los costos monetarios de las invasiones biológicas en el Reino Unido (UK) utilizando una síntesis global de los costos reportados sobre invasiones biológicas. Las especies exóticas invasoras le han costado a la economía del Reino Unido entre US$6,9 mil millones y US$17,6 mil millones (£ 5.4 – £ 13.7 mil millones) en pérdidas y gastos reportados desde 1976. La mayoría de los costos se reportaron a la escala del Reino Unido o Gran Bretaña (97%) y, por lo tanto, la representación de informes de costos a escala individual de cada país dentro del Reino Unido fue escasa. Los informes de invasiones de animales fueron los más costosos ($4,7 mil millones), seguidos por las invasiones de plantas ($1,3 mil millones) y de hongos ($206,7 millones). Los costos de daños reportados (es decir, excluyendo los costos de gestión) fueron más altos en ambientes terrestres ($4.8 mil millones) que en ambientes acuáticos o semiacuáticos ($29.8 millones), afectando principalmente a la agricultura ($4.2 mil millones). Los invasores con introducciones más antiguas acumularon costos totales de invasión significativamente más altos.

Los costos de invasión han aumentado rápidamente desde 1976, lo que le ha costado a la economía del Reino Unido unos $157,1 millones (£122,1 millones) por año, en promedio. La información publicada sobre costos económicos específicos incluyó sólo 42 de las 520 invasores reportados en el Reino Unido y generalmente estaba disponible solo para los taxones más estudiados, con solo cuatro especies contribuyendo con el 90% de los costos específicos de cada especie. Dado que muchas de las especies invasoras que carecen de datos de costos se gestionan activamente y tienen impactos bien conocidos, esto sugiere que la información de costos es incompleta y que los totales presentados aquí son subestimaciones enormes debido a lagunas de conocimiento. El gasto financiero en el manejo de invasiones es una fracción (37%) de los costos incurridos por los daños causados por los invasores; por lo tanto, se requieren con urgencia mayores inversiones en la gestión de especies invasoras del Reino Unido.

#### Abstract in German

Obwohl die hohen Kosten biologischer Invasionen häufig aufgezeigt werden und eine wichtige Motivation für das Umweltmanagement und die Umweltpolitik darstellen, sind synthetisierte Daten rar. Hier quantifizieren und untersuchen wir die monetären Kosten biologischer Invasionen im Vereinigten Königreich anhand einer globalen Synthese der gemeldeten Invasionskosten. Invasive gebietsfremde Arten haben die britische Wirtschaft seit 1976 zwischen 6,9 und 17,6 Milliarden US-Dollar (5,4 bis 13,7 Milliarden Pfund) an gemeldeten Verlusten und Ausgaben gekostet. Die meisten Kosten wurden für das Vereinigte Königreich oder Großbritannien (97%) und damit für das gesamte Land gemeldet. Berichte über invasive Tiere waren die teuersten (4,7 Mrd. USD), gefolgt von Pflanzen (1,3 Mrd. USD) und Pilzen (206,7 Mio. USD). Die gemeldeten Schäden (d.h. ohne Verwaltungskosten) waren in terrestrischen Habitaten (4,8 Mrd. USD) höher als in aquatischen oder semi-aquatischen (29,8 Mio. USD) und wirkten sich hauptsächlich auf die Landwirtschaft aus (4,2 Mrd. USD). Invasoren mit früheren Einführungsjahren verursachten signifikant höhere Gesamtinvasionskosten. Die Invasionskosten sind seit 1976 rapide gestiegen und kosten die britische Wirtschaft durchschnittlich 157,1 Mio. USD (122,1 Mio. GBP) pro Jahr. Zu den veröffentlichten Informationen zu spezifischen wirtschaftlichen Kosten gehörten nur 42 von 520 im Vereinigten Königreich gemeldeten Invasoren, die im Allgemeinen nur für die am intensivsten untersuchten Taxa verfügbar waren, wobei nur vier Arten 90% der art-spezifischen Kosten beisteuern. Angesichts der Tatsache, dass viele der invasiven Arten, denen Kostendaten fehlen, aktiv verwaltet werden und allgemein anerkannte Auswirkungen haben, deutet dies darauf hin, dass die Kosteninformationen unvollständig sind und dass die hier dargestellten Summen aufgrund von Wissenslücken stark unterschätzt werden. Die finanziellen Ausgaben für das Management von Invasionen machen einen Bruchteil (37%) der Kosten aus, die durch Schäden durch Eindringlinge entstehen. Daher sind dringend größere Investitionen in das Management invasiver Arten im Vereinigten Königreich erforderlich.

#### Keywords

England, InvaCost, invasive alien species, non-native species, Northern Ireland, published monetary impacts, Scotland, socioeconomic sector, Wales

## Introduction

Biological invasions can cause far-reaching ecological, environmental, social and economic impacts in invaded ranges (Simberloff et al. 2013; Linders et al. 2019; Pyšek et al. 2020; Diagne et al. 2021). In the last two decades, there has been an increasing number of studies examining the ecological impacts of invasive alien species (hereon, invasive species) (Crystal-Ornelas and Lockwood 2020). However, notwithstanding a few national-scale studies (e.g. Pimentel et al. 2000, 2005; Williams et al. 2010; Hoffman and Broadhurst 2016), the socioeconomic implications have generally lacked synthesis until recently (Bacher et al. 2018; Shackelton et al. 2019; Diagne et al. 2020a; Cuthbert et al. 2021a; Diagne et al. 2021). A lack of cost-reporting reduces monetary incentives for policy-makers to implement management measures aimed at preventing the introduction, spread and impacts of invasions (Diagne et al. 2020b). That is despite management, especially when applied at an early invasion stage (Leung et al. 2002; Ahmed et al. 2021), being highly cost-effective in reducing longer-term management expenditure or damage to resources (Aukema et al. 2011; Paini et al. 2016).

Until recently, large-scale studies into the economic costs of invasive species have been limited to major geographic entities, such as the United States (Pimentel et al. 2000, 2005), Europe (Kettunen et al. 2009) and Australia (Hoffman and Broadhurst 2016). Importantly, these studies have raised societal and policy-maker awareness of the massive economic costs of biological invasions, yet many nations lack assessment. In 2020, the United Kingdom (UK) was the 5$^{th}$ largest economy in the world (World Economic Outlook Database 2020) and has experienced high levels of invasion success (Roy et al. 2014a; van Kleunen et al. 2015), with economic factors, such as GDP, known to influence invasion rates (Lin et al. 2011) and invader economic costs (Haubrock et al. 2021a; Kourantidou et al. 2021).

Despite invasive species being increasingly recognised as a concern for the UK government (EAC 2019), in-depth and up-to-date cost reporting of invasions to the UK economy is lacking. Early estimates of the total cost of invasive species to the UK economy have, however, been made (e.g. White and Harris 2002; Williamson 2002), albeit with a focus on relatively few, well-known taxa. In 2010, invasion costs were estimated at around £1.7 billion per year in England, Scotland and Wales (Williams et al. 2010). In Northern Ireland, invasion costs have been estimated at £46.5 million per year (Kelly et al. 2013). Williams et al. (2010) found that rabbits, Japanese knotweed and wild oats were the costliest invasive species in the UK and agriculture was the most impacted sector, especially in England. Other UK studies have focused on specific environments and cost types. For freshwater invasions in Great Britain, costs of controlling invasive species have been projected at £43.5 million per year in the case of management being undertaken at all invaded locations (Oreska and Aldridge 2011). That pioneering study also highlighted aquatic macrophytes and zebra mussels as two particularly expensive species for management. These same species groups have since been targeted in biosecurity campaigns such as Check, Clean, Dry in the UK (Anderson et al. 2015). However, whilst having raised important awareness, often such studies are outdated, based on extrapolations and have a limited focus on one specific cost type and there thus remains a lack of wide-scale cost estimation for impacts that are empirically observed. There is also no basis to test the notion that observed management investments are less costly than resource damages and losses from invasions in a standardised way, despite Williams et al. (2010) identifying that prevention is cheaper than longer term control in the UK.

Overall, the economic costs of invasions for the UK lack a finer-scale, up-to-date synthesis across multiple environmental, social and temporal contexts, with different types of costs compiled in a comparable way. There have been few appraisals of the biases and knowledge gaps in cost reporting amongst invasive species, despite the presence of 'flagship' invaders in the UK that receive high attention from scientists and media outlets (Roy et al. 2014b). As such, whether costs correlate with the degree of scientific interest towards a given taxon lacks examination. More broadly, invasion science has been shown to be taxonomically biased and only a minority of invasive species are studied in detail (Jarić et al. 2020). This unevenness leads to knowledge gaps in the costs of invasions, which can make management, prioritisation and policy creation difficult. Robust analyses of economic costs are urgently required to enable cost-benefit analyses and efficient allocations of limited economic resources.

The need to comprehensively understand costs of invasive species on the UK economy is particularly crucial given their escalating numbers (Manchester and Bullock 2000; Roy et al. 2014b; Seebens et al. 2017, 2021). The Great Britain Non-Native Species Secretariat estimates that approximately ten new alien species have become established in the UK each year since 1950 and, on average, two of these have become invasive since 2000 (EAC 2019). As the rate of invasion across the UK increases over time, so too are the expected costs associated with these invasions (Diagne et al. 2020a). However, how economic costs relate to the length of time an alien species has been established remains unclear; species that invaded earlier might accrue greater costs or, on the contrary, these costs might diminish as species become naturalised. This needs to be assessed and temporal dynamics in total costs need to be characterised. Likewise, whether certain pathways of introduction are associated with higher costs than others at different times require consideration.

To address these knowledge gaps, we use UK-specific data from 1976 to 2020 in the InvaCost database (Diagne et al. 2020a), a global compilation of the available literature on the economic costs of invasive species. This database compiles detailed cost information suitable for large-scale syntheses of costs associated with invasive species at different spatial, taxonomic and temporal scales. Specifically, we ask:

**Question 1:** What is the reported economic cost of invasive species in the UK and how is it distributed amongst taxonomic groups, habitat types and socioeconomic sectors? Given its economic importance, we expect costs to be higher from species impacting agriculturally-intensive terrestrial environments.

**Question 2:** Are studies and recorded costs shared equally amongst all invasive species? We expect that most costs are caused by relatively few species and that these species are particularly well-known and studied, reflecting a positive feedback between documented costs and study effort.

**Question 3:** How do costs of invasions vary over time and are species with early introductions costlier than more recent invaders considering their introduction pathways? We expect that costs per species will increase with residence time, given a longer time period over which to accrue costs and that common introduction pathways will be dominant (e.g. ornamental; van Kleunen et al. 2020).

Overall, answering these questions allows us to synthesise cost information across numerous ecological and socioeconomic contexts in the UK, helping to make informed current and future management strategies. Further, they will help in pointing out potential biases in available invasion-related cost data and guide further research avenues in this topic.

## Methods

### Data collection and filtering

To estimate the cost of invasive species on the UK economy, we used UK-relevant cost data from the latest available version of the InvaCost database (version 3.0; Diagne et al. 2020a; https://doi.org/10.6084/m9.figshare.12668570) up to the year 2020. We note that InvaCost is a 'living' database that is subject to further additions and improvements. Following the InvaCost protocol (Diagne et al 2020a), all references were retrieved using standardised searches within selected repositories [Web of Science (https://webofknowledge.com/); Google Scholar (https://scholar.google.com/); Google search engine, (https://www.google.com/)] and targeted collection through gathering opportunistic literature and contacting experts and stakeholders. Collected materials were thoroughly assessed to identify relevance and extract cost information. Specifically, titles, keywords, abstracts and full texts were checked hierarchically to ensure that (1) they were in English, as per the language competencies of the review team, (2) they contained at least one cost estimate and (3) each cost estimate was attributed exclusively to invasive species (see Diagne et al. 2020a for full details). InvaCost only includes invasive species for which there are documented economic impacts and our cost analysis reflects that scope. The database effectively defines invasive species as human-introduced alien species that cause some economic cost. Duplicates that reported the same or overlapping costs were also removed from the data. We note that, for the most part, InvaCost includes species that are currently invasive in the UK. However, in some cases, costs pertaining to past successful eradications are included, such as for coypu *Myocastor coypus*. Costs from the Channel Islands, British Overseas Territories and the Isle of Man were excluded to tighten the biogeographical focus. All costs were converted to a common, up-to-date currency (2017 US$); we also provided certain cost estimates in 2017 GBP [1 USD = 0.777 GBP (World Bank 2017 exchange range)].

### Data processing

The period of estimation across reported costs varied considerably, spanning periods of several months to several years. In order to obtain comparable costs, we considered all costs for a period of less than a year as annual costs and re-calculated costs covering several years on an annual basis (i.e. costs accumulated over multiple years were divided amongst those years, giving annual cost estimates). Therefore, costs that spanned multiple years were divided equally amongst those years (e.g. a cost totalling $10,000 over ten years would equal $1,000 per year). If there was no evidence for a cost occurring in more than one year (i.e. *One-time* cost), we conservatively counted it for one year only and likewise for costs that were *Potentially-ongoing* (Occurrence column in InvaCost). In cases where the timespan for the costs was not described in the data publication, we used publication year as a surrogate for starting year and – if the cost was *Potentially-ongoing* – publication year as a surrogate for ending year.

The conversion of all costs into an annual basis resulted in a total of 709 expanded entries (Suppl. material 1; 353 initial entries). This was accomplished using the *expandYearlyCosts* function of the 'invacost' package version 0.3–4 (Leroy et al. 2020) in R version 4.0.2 (R Core Team 2020); this function considers both the probable starting and ending years of each cost entry in the InvaCost database to annualise costs (see Suppl. material 2; https://doi.org/10.6084/m9.figshare.12668570). The first cost entry in our dataset was recorded in 1976, so all analyses were performed for the period 1976 to 2019, because that was the last year with robust reported costs. Costs in InvaCost are reported at different spatial scales (Spatial scale column), from site-specific to regional and national estimates. We carefully considered this information and checked for potential duplications in costs within or amongst scales, with costs estimated at all spatial scales (i.e. unit, site or country) included in the analyses.

## Question 1: Invasion costs distributions through space and sectors

We categorised the invasion costs using seven criteria. The first two criteria were used to filter and subset the costs and the other five were used in analysis. See Suppl. material 2 for further information on the considered categories.

(i) Method reliability (*High* or *Low*): Cost estimates, extracted from peer-reviewed publications or official reports or with documented, repeatable and/or traceable methods, were considered to have *High* reliability; all other estimates were designated as *Low* reliability (Diagne et al. 2020a);

(ii) Implementation (*Observed* or *Potential*): Cost estimates that occurred in the invaded habitat were designated *Observed* and those or that were extrapolated or predicted to occur were deemed *Potential*.

We calculated full costs, which include potential and low reliability estimates, but excluded these more speculative estimates when examining the data in detail (as well as for the following subsections). The more detailed, conservative analysis, therefore, considered only the following descriptors:

(iii) Country (*England*, *Scotland*, *Wales*, *Northern Ireland*). Where costs were attributed to a particular country, we presented costs to that country; other costs were recorded as spanning multiple countries, i.e. *Great Britain* (i.e. excluding Northern Ireland) or the *UK* (i.e. including Northern Ireland);

(iv) Environment of the invasive species (*Terrestrial*, *Aquatic*, *Semi-aquatic* or *Diverse/Unspecified*): the habitat from which the species causing the cost originated. Here, we considered that *Semi-aquatic* corresponds to species that are closely associated with water for development, reproduction and/or foraging (e.g. *M. coypus* is a semi-aquatic rodent);

(v) Type of cost: (a) *Damage* referring to damages or losses incurred by invasion (e.g. costs for damage repair, resource losses, medical care), (b) *Management* comprising control-related expenditure (e.g. monitoring, prevention, management, eradication) and money spent on education, research and maintenance costs, (c) *Mixed* including mixed damage and management costs (cases where reported costs were not clearly distinguished amongst cost types);

(vi) Impacted sector: the activity, societal or market sector that was impacted by the cost (*Agriculture*, *Authorities-Stakeholders*, *Environment*, *Fishery*, *Forestry*, *Public and social welfare*); individual cost entries not allocated to a single sector were classified as *Mixed*;

(vii) Kingdom: the taxonomic kingdom of the species associated with each cost entry. Where this information was missing, taxa were deemed to be *Diverse/Unspecified*. Viruses were included as a general 'kingdom', but only counted if they were vectored by an invasive species in the UK subset (e.g. squirrelpox virus vectored by the grey squirrel *Sciurus carolinensis*).

## Question 2: Taxonomic biases in invasion costs

To identify the proportions of invasive species in the UK for which cost data are available, the list of individual species in InvaCost was compared with comprehensive lists of invasive species in the UK. Lists of known invasive species were extracted and compiled for the UK from the following databases: (1) InvaCost version 3.0; (2) the Global Invasive Species Database (GISD); (3) the sTwist database; and (4) the Great Britain Non-native Species Information Portal (GB-NNSIP) (Table 1). Only species listed within the UK were extracted from each database, with listed species checked to confirm their alien status and refined accordingly. We classify all of these species as "invasive", but note that the definitions of invasiveness differ slightly amongst these datasets (Table 1). We used the GBIF.org Backbone Taxonomy to standardise species names.

Rank-abundance analyses were used to determine the unevenness of species' costs according to cost types (management and damage), environments (aquatic, semi-aquatic and terrestrial) and kingdoms (plants and animals).

A keyword search on the Web of Science over the period 1960 to 2020 was used to quantify research effort (i.e. publication numbers) towards individual species listed as invasive in the UK (Table 1). Global and UK-only searches were conducted to determine research effort, as indicated by numbers of publications. The Global search string used species' scientific names only; the UK-only search string combined the scientific name of the species with "UK" OR "United Kingdom" OR "Great Britain" OR "England" OR "Scotland" OR "Wales" OR "Northern Ireland". For example, the search string used to retrieve the number of studies for *Oryctolagus cuniculus* was: TS=("Oryctolagus cuniculus") AND TS=("UK" OR "United Kingdom" OR "Great Britain" OR "England" OR "Scotland" OR "Wales" OR "Northern Ireland"), where TS is the "Topic". The results and specific search terms are provided in Suppl. material 3.

We used a Kruskal-Wallis test to compare research efforts for invasive species that were present vs. absent from InvaCost. This tested the null hypothesis that research effort was equal across species with and without published impact costs. We also used

**Table 1.** Initial numbers of known invasive species extracted from the InvaCost, GISD, sTwist and GB-NNSIP databases for the UK. Definitions of invasiveness are provided in relation to each database, along with underlying sources of data extracted.

| Database | Species (*n*) | Invasive definition | Data source |
|---|---|---|---|
| InvaCost | 42 | Invasive alien species with reported economic impacts. | Version 3.0, Diagne et al. (2020a; https://doi.org/10.6084/m9.figshare.12668570). |
| GISD | 216 | Alien species with known negative impacts on biodiversity in the region where they are invasive. | GISD (www.iucngisd.org/gisd). |
| sTwist | 321 | A taxon whose introduction and/or spread threatens biological diversity (Convention on Biological Diversity). | Version 1.2.3, https://doi.org/10.5281/zenodo.3763222. Underlying data sources: Caphina et al. (2017); GAVIA (Dyer et al. 2017); Global Alien First Records Database (Seebens et al. 2017); GloNAF (van Kleunen et al. 2015); GRIIS (available via: GBIF.org). |
| GB-NNSIP | 282 | An introduced taxon designated as having a negative ecological or human impact. | Roy et al. (2014b). |

linear regression to test the relationship between species' total economic costs and their research effort, on a $\log_{10}$ scale to normalise residuals and homogenise variances. Here, a significant positive relationship would indicate that greater invasion costs are reported for invasive species with larger numbers of studies.

### Question 3: Temporal dynamics of invasion costs

The cost over time of all UK invasive species was calculated via the *summarizeCosts* function of the 'invacost' R package (Leroy et al. 2020). This function illustrates the dynamics of costs over time, projecting the mean cost per decade, as well as the mean cost over the entire reported period (i.e. from 1976 to 2019; the last year with robust, reported costs).

Using first record information from the sTwist database, we used linear regression to examine the relationship between the length of time a species has been reported as invasive in the UK and its total invasion cost. First record information was available for 35 species reported in InvaCost (of the 42 species with individual cost entries). Both time since introduction and total economic costs were modelled on a $\log_{10}$ scale to normalise residuals and homogenise variances. We thus tested whether species with an earlier year of introduction accrued greater impacts than species that were introduced more recently. For each species and year of introduction, we also examined introduction pathway information (Suppl. material 4), as reported in the DAISIE database (Roy et al. 2020). This database is an inventory of invasive species in Europe, in the form of a checklist; we used UK-specific data only.

## Results

### Question 1: Invasion costs distributions through space and sectors

Biological invasions cost the UK economy an amount estimated from \$6.9 billion to \$17.6 billion (£5.4 billion – £13.7 billion) between 1976 and 2019. The lower, more conservative cost estimate excludes *Potential* costs ($5.2 billion; £4.0 billion; 103 entries) and *Low* reliability costs ($5.5 billion; £4.3 billion; 101 entries). We use the more conservative estimates for all further analyses below (538 entries).

Of the total for the whole of the UK, $4.3 billion (£3.3 billion) was attributed to the UK and $2.4 (£1.9 billion) billion to Great Britain. Much lower cost totals were recorded per country, with $81.5 million (£63.3 million) to Northern Ireland, $76.2 million (£59.2 million) to England, $34.9 million (£27.1 million) to Scotland and $2.4 million (£1.9 million) to Wales. Therefore, the vast majority of invasion costs were reported at larger spatial scales.

Where costs were assigned to specific taxa, the majority were attributed to animals ($4.7 billion, 267 entries; including $2.4 billion to mammals and $1.5 billion to insects), followed by plants ($1.3 billion, 99 entries) and then fungi ($206.7 million, 2 entries). Invasive chromists (16 entries) and viruses (10 entries) cost $771,575 and $775,451, respectively. However, a large sum of invasion costs in the UK was either not taxonomically defined or spanned multiple kingdoms (i.e. *Diverse/Unspecified*; $781.6 million, 144 entries).

Terrestrial habitats were most impacted overall ($6.4 billion, 245 entries) and had the highest number of cost entries. Impacts to aquatic ($258.5 million, 116 entries) and semi-aquatic habitats ($51.7 million, 86 entries) were, respectively, one and two orders of magnitude lower (Fig. 1), despite high numbers of cost entries. A relatively small portion of total economic costs was reported from entries that affected multiple or unspecified environment types ($172.0 million, 91 entries) (Fig. 1).

The costliest impacts of invasions in the UK were incurred by the agricultural sector ($4.9 billion, 32 entries), followed by authorities and stakeholders (i.e. governmental services and/or official organisations, $955.9 million, 436 entries), mixed sectors ($824.6 million, 41 entries), as well as forestry ($144.2 million, 11 entries). Public and social welfare ($37.8 million, 10 entries), fisheries ($11.0 million, 5 entries) and the environment ($7.8 million, 3 entries) were reportedly impacted to a much lesser degree. Agricultural, mixed and forestry impacts were typically incurred through direct damage or losses to resources, whilst impacts to authorities and stakeholders were mostly related to management expenditure. Across these sectors and cost types, terrestrial environments were dominant, with relatively few contributions from aquatic and semi-aquatic environments overall in terms of invasion costs. In contrast to terrestrial environments, where costs were mostly damage-related, aquatic and semi-aquatic costs were more likely to be from management actions (Fig. 1).

## Question 2: Taxonomic biases in invasion costs

Overall, cost data in the UK were reported for 42 invasive species in InvaCost (with individual cost entries; $n$ = 56 including species within 'mixed' entries). However, there were 520 unique invasive species in the UK reported in InvaCost, sTwist, GISD or GB-NNSIP, thus meaning that approximately 8% of known invasive species in the UK have documented economic costs (Fig. 2a). Invasive species with reported cost data

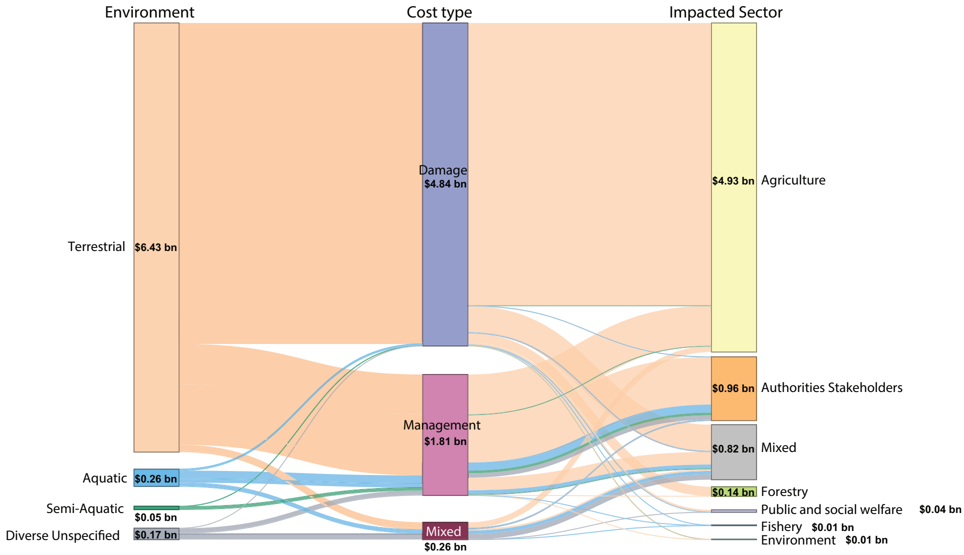


**Figure 1.** Alluvial plot illustrating flows of identified invasion cost types in the UK amongst environments and socioeconomic sectors. Abbreviations: bn is billion (2017 US$).

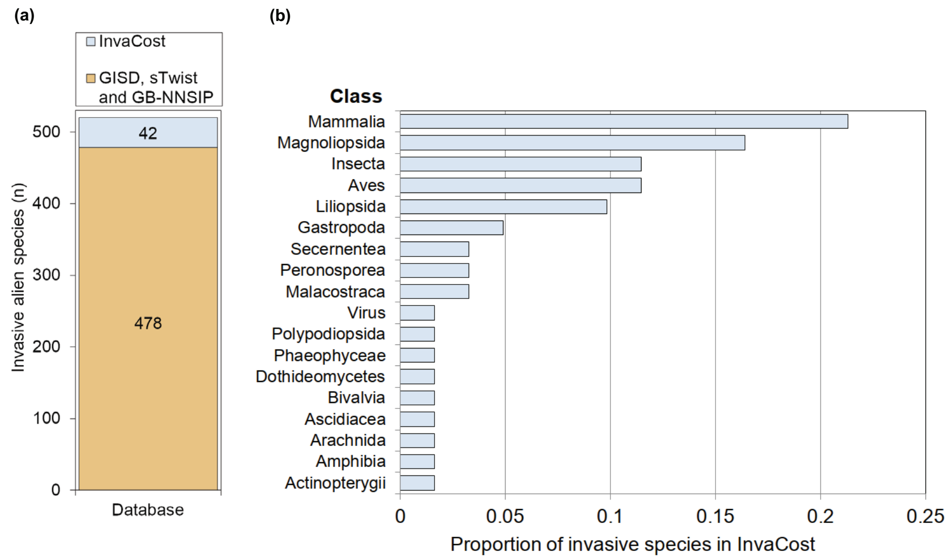


**Figure 2.** Barplots showing **a** total numbers of all known invasive species in the UK (i.e. species within GISD, sTwist and GB-NNSIP) and UK invasive species in InvaCost; and **b** proportions of UK invasive species in InvaCost across classes.

mainly belonged to the Mammalia (21%), Magnoliopsida (16%), Insecta (11%) and Aves (11%) classes (Fig. 2b).

Cost contributions were highly uneven across species overall (Fig. 3). Considering total costs, the European rabbit *O. cuniculus* contributed 62%, followed by Japanese

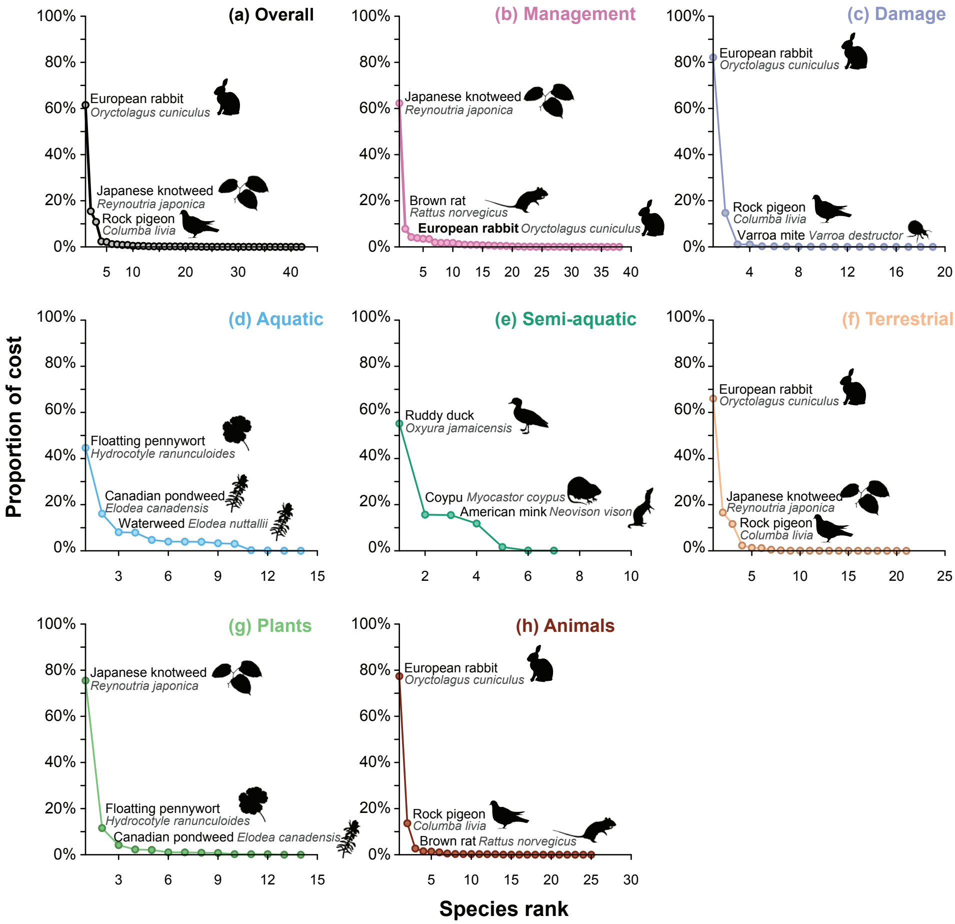


**Figure 3.** Whittaker plots illustrating ranked proportional cost contributions across species for **a** overall **b** management **c** damage **d** aquatic **e** semi-aquatic **f** terrestrial **g** plant and **h** animal cost categories. The top three highest-contributing species are labelled on each subplot, for example, the European rabbit ranks as the costliest species **a** overall, for **c** damage costs and amongst the terrestrial organisms (**f**) and animal kingdom (**h**), representing 62%, 82%, 66% and 77% of costs in the respective categories. Note the differences in *x*-axes scaling.

knotweed (*Reynoutria japonica*) and the rock pigeon (*Columba livia*). Japanese knotweed dominated management costs (62%), followed by the brown rat (*R. norvegicus*) and European rabbit. Damage costs were again dominated by the European rabbit (82%), followed by the rock pigeon, with Varroa mite (*Varroa destructor*) third.

Aquatic environments were mostly impacted by floating pennywort (*Hydrocotyle ranunculoides*) (45%) and Canadian pondweed (*Elodea canadensis*) (16%), thereafter waterweed (*Elodea nuttallii*). Semi-aquatic taxa costs were mostly driven by the ruddy duck (*Oxyura jamaicensis*) (55%), coypu (*Myocastor coypus*) and American mink (*Neovison vison*). Costs in terrestrial environments were driven predominantly by the European rabbit (66%), Japanese knotweed and rock pigeon. Overall, the majority of spe-

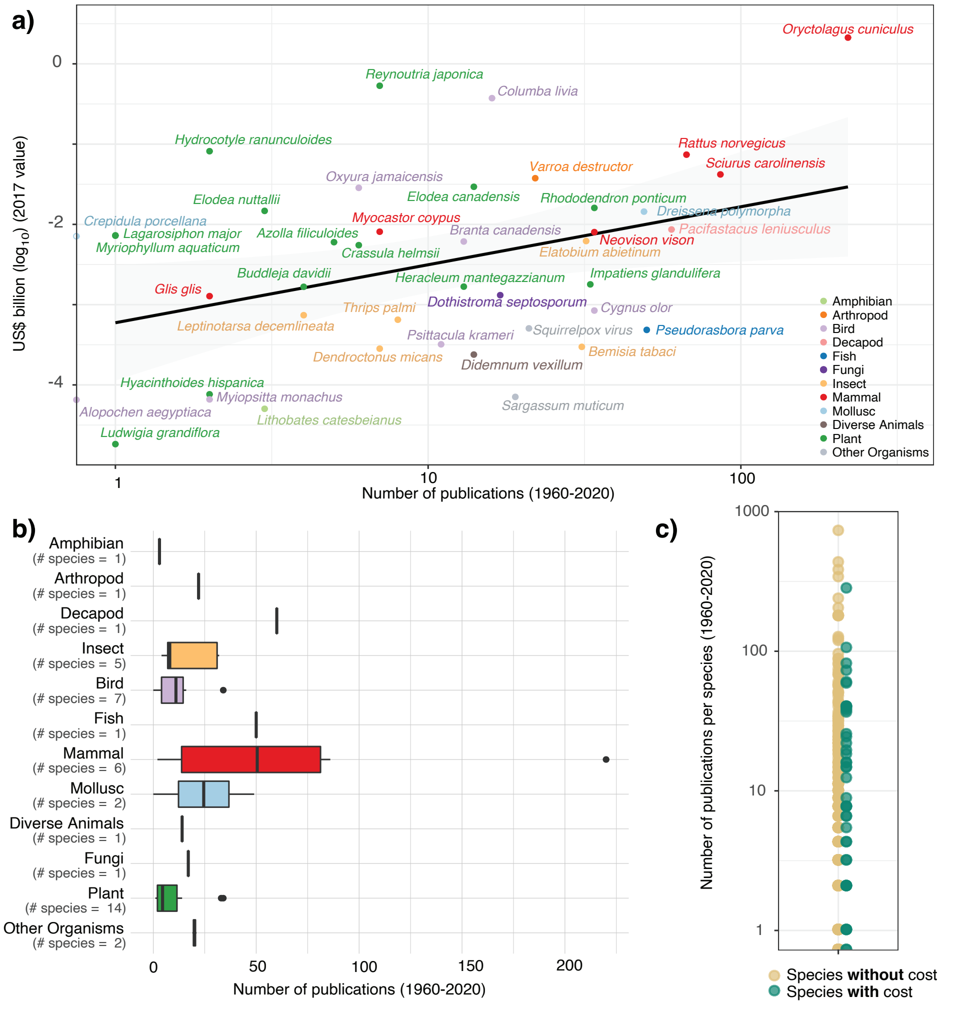


**Figure 4.** Per-species invasion costs and study efforts showing **a** the number of publications available in Web of Science for the period 1960–2020 for each species with InvaCost records against the total cost for each species in billion US$ (2017 value; $log_{10}$ scale; shaded area is 95% confidence interval) **b** the distribution of the number of publications available in Web of Science for the period 1960–2020 for each species with invasion costs by organism group ("# species" refers to numbers of species in InvaCost within that group) and **c** distribution of publication numbers of invasive species with and without costs.

cies with monetary costs (83%) each contributed less than 1% of the respective total cost (Fig. 3). Costs of the European rabbit were incurred predominantly by agricultural impacts (93%); Japanese knotweed through impacts to authorities and stakeholders (97%); and rock pigeon towards mixed sectors (100%).

Invasive species with economic costs were associated with significantly more publications than UK invasive species without costs ($\chi^2 = 32.79$, df = 1, $p < 0.001$; Suppl. material 5: Fig. S1; Fig. 4). Of those invasive species present in InvaCost, total per-

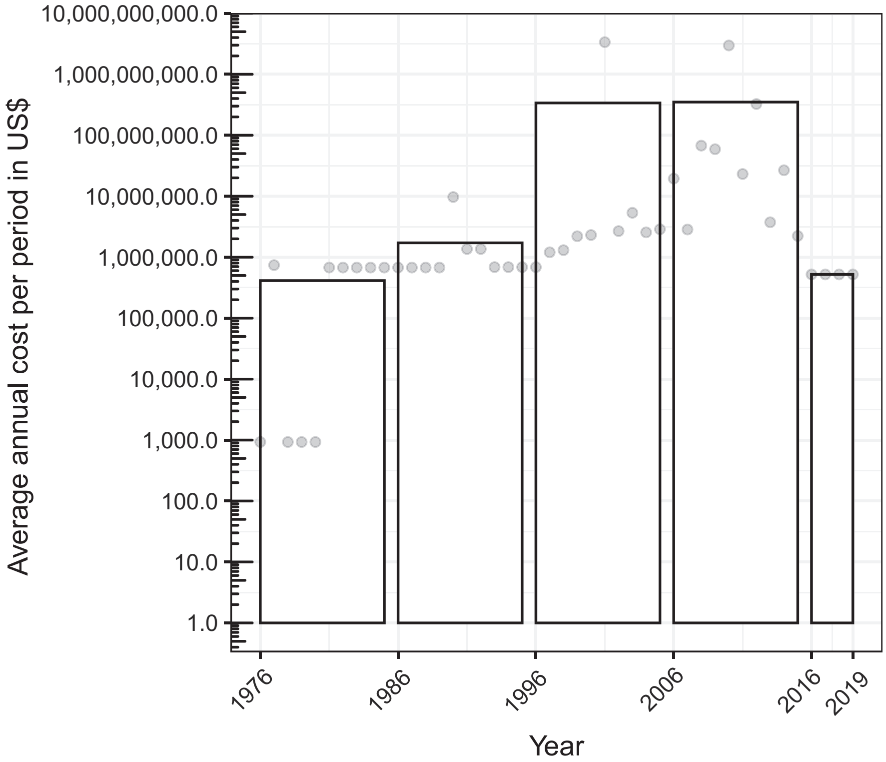


**Figure 5.** Annual average costs of biological invasions in the United Kingdom, considering decadal means (except 2016 to 2019: four years mean). Grey points indicate annual total costs. Note the *y*-axis is on a $\log_{10}$ scale.

species costs were positively related to numbers of studies per species ($t = 3.32$, $p < 0.01$; Fig. 4a). Plants, birds, mammals and insects had the highest numbers of species with costs (Fig. 4b), whilst many other taxa comprised just one species. Plants had relatively few publications per species, yet many invasive plants exhibited high costs relative to their study effort (e.g. floating pennywort, *H. ranunculoides*; Japanese knotweed, *R. japonica*). For birds, the rock pigeon (*C. livia*) and ruddy duck (*O. jamaicensis*) had the highest costs relative to publications. Mammals were generally the focus of the most published studies, with taxa such as the coypu (*M. coypus*) and European rabbit (*O. cuniculus*) having especially high costs relative to their study intensity (Fig. 4).

## Question 3: Temporal dynamics of invasion costs

In examining the raw cost trends over time, between 1976 and 2019, the accumulated costs of \$6.9 billion (\$157.1 million per year; £5.4 billion and £122.1 million, respectively) increased steadily until 2005, being between \$411,987 (1976–1985) and \$1.7 million (1986–1995) per year until 1995. Costs then grew rapidly to between \$338.7 million and \$350.0 million per year after 1995 (Fig. 5). Cost reporting reduced in

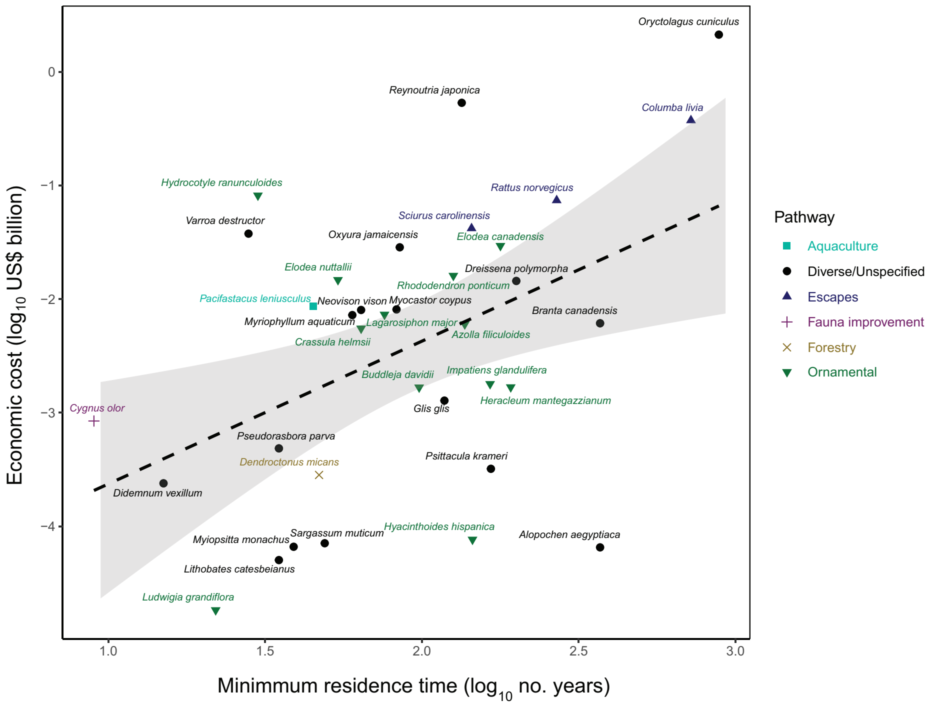


**Figure 6.** Invasion costs (US$ billions) as a function of number of years since introduction for UK invasive species. Note that both the *x*- and *y*-axes are on a $\log_{10}$ scale. The dashed line represents a linear regression model fit and the shaded area the 95% confidence interval. Pathways of introduction per species are indicated by different fill shapes and colours.

recent years, causing lower average costs in the last four years, likely due to time lags in cost reporting.

Of the 35 UK invasive species present in InvaCost with first record information, there was high variation in species' costs ($18,300 to $2.12 billion) and minimum residence times (9 to 885 years; time since first record of introduction; Fig. 6). Nonetheless, species that have been present in the UK for longer tended to have significantly higher invasion costs ($t$ = 2.93, $p$ < 0.01). There were several anomalies, however, to this trend, with species, such as the floating pennywort (*H. ranunculoides*), Varroa mite (*Varroa destructor*) and European rabbit (*O. cuniculus*), displaying disproportionately high impacts relative to their minimum residence time. Conversely, species, such as the Egyptian goose (*Alopochen aegyptiaca*), Spanish bluebell (*Hyacinthoides hispanica*) and edible dormouse (*Glis glis*), had relatively low economic effects, despite their early record of introduction (Fig. 6).

Of the five specified pathways of UK invasive species introductions, species introduced via the ornamental pathway were most common (12 species), followed by escapes (3 species); almost half of species were introduced via multiple (diverse) or unspecified pathways (17 species). In turn, diverse and unspecified pathways contributed the greatest costs ($2.8 billion), followed by escapes ($0.49 billion) and ornamental species ($0.17 billion). There was, however, generally no trend between pathway prevalence and minimum residence time for the assessed UK invasive species (Fig. 6).

## Discussion

Biological invasions have cost the UK economy at least $6.9 billion (£5.4 billion) since 1976 and possibly at least $17.6 billion (£13.7 billion) if we include low reliability and potential costs (Diagne et al. 2020a). Costs have been rising rapidly over time and species with longer residence times have accrued higher invasion costs. However, there were no cost estimates for 90% of invasive species recorded so far in the UK. Of the costs reported for individual species, 90% were caused by approximately 10% of all invasive species in the UK with costs. Although the more costly species are also the most studied, the lack of any cost data for the majority of invasive species suggests that knowledge gaps are pervasive and that total costs of invasive species in the UK are underestimated. If cost reporting was complete for all invasive taxa, activity sectors, geographic regions and through time, UK invasion costs would likely be far greater than those reported here. Our totals also exclude invasion costs based on extrapolations or predictions ($5.2 billion), which calls for further research effort to decipher economic costs empirically. Impacts to certain activity sectors, such as fisheries and the environment, require urgent quantification, given the available means of quantifying economic impacts from environmental degradation and losses of ecosystem services from invasions (Hanley and Roberts 2019).

### Question 1: Invasion costs distributions through space and sectors

Invasion costs were mostly reported at UK or Great Britain scales and, thus, further cost reporting is required at country-level scales or lower within the UK to improve and pinpoint management actions. Most costs stemmed from direct damage rather than management spending and principally impacted the agriculture sector. This dominance of damage-related costs over management aligns with trends in other geographic regions worldwide (Crystal-Ornelas et al. 2021; Haubrock et al. 2021a; Heringer et al. 2021; Liu et al. 2021). Invasion impacts in the UK were largely driven by animals, which were both the most studied and costliest taxa. Terrestrial invasion costs were most frequently documented and accounted for 93% of reported impacts overall. Contrastingly, there were comparatively few studies documenting economic impacts of aquatic and semi-aquatic invasions, despite the presence of multiple aquatic invaders that are recognised as a high management priority in the UK (e.g. Oreska and Aldridge 2011; Booy et al. 2020) and high global aquatic invasion costs (Cuthbert et al. 2021a). This trend might also reflect broader research biases within ecology towards terrestrial over aquatic environments (Menge et al. 2009; Cuthbert et al. 2021a) or perhaps reflect that aquatic invasion costs are more difficult to be observed empirically and thus likely to be predicted (and therefore excluded from our data subset).

Reported management costs were substantially lower than reported damage costs. Management costs were primarily incurred by authorities and stakeholders that are responsible for ecosystem management practices in the UK, rather than through primary sectors (e.g. agriculture and forestry). Aquatic and semi-aquatic invaders were more likely to incur management costs than direct damage, but the converse was true for terrestrial species. A study by Oreska and Aldridge (2011) found that aquatic invaders cost Great Britain £26.5–£43.5 million per year; like our study, most costs were attributed to macrophytes and bivalves. This suggests that observed management cost totals for aquatic systems ($258.5 million since 1976; £200.9 million) in our study may be underestimated. Nonetheless, aquatic invasion costs were found to be at least one order of magnitude lower than terrestrial impacts overall. A similar finding has been made at the global scale, where aquatic invasion costs have been found to have reached over $20 billion in the year 2020 alone, but remain an order of magnitude lower than terrestrial invasion costs in total (Cuthbert et al. 2021a). A lack of observed aquatic invasion costs in the UK may stem from a paucity in damage reporting from aquatic taxa or suggest that aquatic invasion costs are more likely to be predicted or extrapolated, given the difficulty in monitoring submerged environments. Awareness campaigns such as Check, Clean, Dry have spearheaded aquatic biosecurity in the UK, with recent methods developed to improve invader decontaminations (Anderson et al. 2015; Bradbeer et al. 2020). Recent criticisms have, however, been raised surrounding the efficacy of existing biosecurity protocols to prevent aquatic invasions and invasive species secondary spread across Europe (Coughlan et al. 2020).

More effective and coordinated management strategies are required to help limit future invasion costs in the UK, particularly in the terrestrial realm where damages are most burgeoning. Such management strategies should consider the range of pathways through which costly invaders have established (Robertson et al. 2020), as well as scientific evidence which indicates the most damaging species. Proactive management strategies, such as biosecurity, can prove disproportionately more cost-effective than longer-term, reactive interventions at more advanced invasion stages (Leung et al. 2002; Williams et al. 2010; Ahmed et al. 2021). Moreover, nations that fail to develop sufficient management strategies, at any invasion stage, could incur greater resource damages and losses as a result of biological invasions, such as through impacts to agriculture, forestry and human health sectors (Aukema et al. 2011; Paini et al. 2016).

Similar to prior estimates of UK invasion costs (Williams et al. 2010), we found the agricultural sector to be the most impacted overall and with cost types dominated by damages and losses, principally by animals. More broadly, this trend is congruent with a growing threat to agricultural enterprises worldwide by invasive species, threatening food production (Paini et al. 2016). Economic impacts were accordingly dominated by taxa affecting agriculturally-intensive terrestrial environments (e.g. European rabbit, brown rat, Varroa mite), where damage can be more readily perceived than in submerged realms. These results also corroborate Williams et al. (2010), where economic impacts from rabbits were dominant in the UK. Indeed, most studies on UK invasive species have focused on invasive mammals, despite alien plants constituting the highest number of alien species established by far (Roy et al. 2014b). Other studies have highlighted the extent of knowledge gaps (in terms of understudied taxonomic groups, regions and habitat types), indicating that previous invasion cost quantifications could be gross underestimates at the global scale (Bradshaw et al. 2016; Diagne et al. 2020a; Diagne et al. 2021).

## Question 2: Taxonomic biases in invasion costs

Across all habitat types and taxonomic groups, where reported, invasion costs in the UK were always dominated by very few species. Similar trends have been found in other countries, with costs dominated by few species in, for example, Italy (Haubrock et al. 2021b), Singapore (Haubock et al. 2021c), Brazil (Adelino et al. 2021) and Argentina (Duboscq-Carra et al. 2021), as well as on the global scale (Cuthbert et al. 2021b). Strikingly, 90% of costs were attributable to just four individual species in the UK. Disproportionately high costs were associated with European rabbit, Japanese knotweed, rock pigeon and floating pennywort, corroborating other UK estimates (Williams et al. 2010). These species were particularly costly compared to their research effort. The disproportionate cost data, which represent 8% of the total invasive species pool in the UK, are somewhat indicative of the Tens Rule.

The Tens Rule hypothesizes that, where 10% of introduced species invade, 10% of those species naturalise and 10% of those become invasive (Williamson 1996). Whilst our results suggest that this hypothesis might be extended to the economic cost incurred by invasive species, absence of information does not indicate absence of impact. Accordingly, this fraction may reflect study effort rather than distribution of economic impacts. Indeed, studies have found much greater invasion success rates than predicted by the Tens Rule, with a success rate of 50% at each invasion stage shown for vertebrates (Jeschke and Strayer 2005). Moreover, the Tens Rule has been stated to be more of an indicator of lack of understanding, than the actual ratio of species that precipitate impacts (Jarić and Cvijanović 2012).

We also note that, because species present as part of 'mixed' cost entries were excluded from species-specific analyses here, numbers of invaders with costs would be higher with their inclusion (totalling 56 species with these 'grouped' costs). Nevertheless, the biases in cost reporting evidenced here were due to sustained focus on a few species, notwithstanding the substantial number of invasive species that are absent from InvaCost. In particular, mammals represented the class with the greatest proportion of reported invasive species with costs, despite not being the most diverse group of invaders in the UK (Roy et al. 2014b).

Cost reporting is lacking for many less notorious invasive species, evidenced by the relationship between those species with reported costs also having a greater number of studies. In the UK, some of the most notorious invaders that feature in targeted management campaigns do not have accessible cost data. The killer shrimp

(*Dikerogammarus villosus*) and quagga mussel (*Dreissena bugensis*) have no reported costs in the UK in InvaCost, despite being amongst 'keystone' invasive species targeted through management campaigns, such as Check, Clean, Dry (Anderson et al. 2015), launched by the UK Government's Department of Environment, Food and Rural Affairs in 2010. Another example is the topmouth gudgeon *Pseudorasbora parva*, which was introduced into the UK in 1985; a species which has been managed to curtail disease risk at high cost (Gozlan et al. 2010; Britton et al. 2011). Similarly, there were no reported costs for the Asian hornet (*Vespa velutina*) (Keeling et al. 2017; Barbet-Massin et al. 2020) nor the ash dieback fungus (*Hymenoscyphus fraxineus*) (Broome et al. 2018), despite their impact and concurrent management responses. The 2019 Environmental Audit Committee recognised a lack of consolidated information across UK organisations for these and other invasive species. This can lead to lost opportunities in managing new invasions in the UK, such as the delayed response in tackling the arrival of oak processionary moth (*Thaumetopoea processionea*) in 2006 (EAC 2019). This now established invasive species is a serious concern for forestry and public health and its unpredictable outbreaks make it difficult and costly to manage (Godefroid et al. 2020).

Overall, relative to three of the most robust databases of invasive species in the UK and beyond (sTwist, GISD and GB-NNSIP), numbers of species represented in InvaCost comprised less than one tenth and the few which are present reflect a bias towards intensively studied invasive species. These numbers also exclude species that are not yet reported as being alien in the UK or those that are introduced or naturalised and not invasive; the mismatch between numbers of invaders present and numbers economically appraised is therefore likely to be vast.

## Question 3: Temporal dynamics of invasion costs

Over half of invaders with individual costs and first records have only been present in the UK for under 100 years. Despite marked species-specific variabilities, our results show that taxa present for longer (i.e. > 100 years) generally have more potential to accrue invasion costs, further highlighting that early-stage management measures are likely to be most cost-effective (Leung et al. 2002, Robertson et al. 2020; Ahmed et al. 2021). In that vein, early-stage prevention has been shown to be hugely more efficient than post-invasion management strategies in the UK (Williams et al. 2010). Furthermore, invasion costs across the UK are increasing rapidly through time, by at least three orders of magnitude since 1976.

Although our overall average annual cost estimate for the whole of the UK since 1976 ($157.1 million; £122.1 million) and, even in the most recent years, is considerably lower than previous estimates (GB: £1.7 billion; Williams et al. 2010), this is likely because prior works did not account for temporal dynamics. We also included only the most robust subset of estimates characterised by being of high method reliability and being empirically observed, i.e. not extrapolations or predictions. In contrast to those previous studies, our cost acquisition methods were centralised and standardised across a comprehensive suite of predictors (Diagne et al. 2020a), improving their comparability.

Given alien species incursions are expected to increase by 36% globally in the next three decades (Seebens et al. 2021) and costs are rising worldwide (Diagne et al. 2021; Cuthbert et al. 2021a), we expect UK costs to increase by further orders of magnitudes in coming years, with factors, such as climate change, as well as trade and transport intensifications, driving invasion rates (Bellard et al. 2013; Seebens et al. 2018; Hulme 2021).

Costs have been rising over time and species with longer residence times had higher costs. Even without further invasions, this means that costs in future will continue to accumulate (signalling an invasion economic impact debt; Essl et al. 2011). Whilst several pathways were identified in the present study, many species were from multiple or unspecified pathways. Nonetheless, the ornamental trade was especially pervasive considering numbers of introductions of costly invasive plants (van Kleunen et al. 2020). This trade activity is known to be increasing over time, with the UK market based on more than 73,000 plant species and varieties (Perrings et al. 2005). In contrast, most animal invasions were through diverse or unspecified pathways or via escapes from captivity (e.g. via pet trade). Horizon scanning has additionally identified a range of high risk invaders that are likely to arrive in the coming years, with 93 identified as constituting at least a medium risk of arriving, establishing and threatening ecosystems (Roy et al. 2014a). We, therefore, expect costs to increase markedly also because many new invaders will arrive in the UK. Indeed, recent UK invaders have shown an ability to rapidly establish and spread and cause impact, such as ash dieback fungus (Broome et al. 2018); with ash accounting for ~ 34 million $m^3$ of the timber volume in UK woodlands, the potential impacts could be massive (Broome et al. 2014). Further, the Asian hornet, which was first known to have arrived in 2016, has been the subject of rapid response control measures in the UK and has the potential to spread rapidly in mainland areas, threatening economically-important pollinators, such as bees (Keeling et al. 2017; Barbet-Massin et al. 2020).

## Conclusion

Despite long-standing knowledge of ecological impacts of invasive species in the UK (Manchester and Bullock 2000), economic costs of invasions have been quantified for less than 10% of the UK's invasive species (42/520 species). If we were to consider species not yet reported as alien in the UK or those that have been introduced, but not yet invasive (Seebens et al. 2017), the proportion of alien species for which we have cost data becomes even smaller. For taxa with reported costs, cost contributions were highly unequally distributed, with infamous and well-studied invaders dominating costs. We acknowledge that not all invaders will cause discernible economic impacts. However, given the striking absence of cost data for species that are known to yield high economic costs (e.g. killer shrimp, Asian hornet, quagga mussel, ash dieback fungus), the general absence of cost data for the great majority of invasive species in the UK seems to point to a lack of data rather than a lack of costs. As such, it is likely that the reported costs, presented in this study, vastly underestimate the true cost of invasions in the UK. Accordingly, we urge greater cost reporting for all known invasive species in the UK and at sufficient resolution to provide information for efficient management practices at local and regional scales. This would enable greater awareness of the costs of UK invasions, supporting and motivating greater investment in management, as well as policy aimed at reducing the economic burden of damage and losses caused by current and future invasive species.

## Acknowledgements

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## Supplementary material 1

**Subset of InvaCost database used for analyses of UK invasion costs. Note that cost data are not annualised.**

Authors: Ross N. Cuthbert, Angela C. Bartlett, Anna J. Turbelin, Phillip J. Haubrock, Christophe Diagne, Zarah Pattison, Franck Courchamp, Jane A. Catford

Data type: database



Link: https://doi.org/10.3897/neobiota.67.59743.suppl1

## Supplementary material 2

**Summary of the content of the descriptive columns of the database used in this study (adapted from Diagne et al. 2020a)**

Authors: Ross N. Cuthbert, Angela C. Bartlett, Anna J. Turbelin, Phillip J. Haubrock, Christophe Diagne, Zarah Pattison, Franck Courchamp, Jane A. Catford

Data type: explanation



Link: https://doi.org/10.3897/neobiota.67.59743.suppl2

## Supplementary material 3

**Web of Science search terms for UK invasive species publication numbers, alongside resulting study numbers**

Authors: Ross N. Cuthbert, Angela C. Bartlett, Anna J. Turbelin, Phillip J. Haubrock, Christophe Diagne, Zarah Pattison, Franck Courchamp, Jane A. Catford

Data type: database



Link: https://doi.org/10.3897/neobiota.67.59743.suppl3

## Supplementary material 4

**Total costs of species with individual cost entries, alongside first record years and introduction pathways**

Authors: Ross N. Cuthbert, Angela C. Bartlett, Anna J. Turbelin, Phillip J. Haubrock, Christophe Diagne, Zarah Pattison, Franck Courchamp, Jane A. Catford

Data type: database



Link: https://doi.org/10.3897/neobiota.67.59743.suppl4

## Supplementary material 5

**Figure S1**

Authors: Ross N. Cuthbert, Angela C. Bartlett, Anna J. Turbelin, Phillip J. Haubrock, Christophe Diagne, Zarah Pattison, Franck Courchamp, Jane A. Catford

Data type: figure

Explanation note: Boxplots of the number of publications recorded in Web of Science for species listed as invasive in the United Kingdom (UK) in the Global Invasive Species Database (GISD), sTwist database and Great Britain Non-native Species Information Portal (GB-NNSIP), but with no specific cost records in InvaCost (beige) and for invasive species with cost records in the UK in InvaCost (green).



Link: https://doi.org/10.3897/neobiota.67.59743.suppl5